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## THE ACCESSORY BLADDERS OF THE TESTUDINATA.

FRANK W. PICKEL.

*Historical.* — More than a century ago Von Perrault (14) mentioned the occurrence of two coecal sacs, emptying into the cloaca in turtles. Later these sacs were drawn and described by Bojanus (4) in *Emys europaea* Schweigg. (*Emys orbicularis* Boulenger), and subsequently an account of them was published by Lesueur (10). According to the latter author these sacs, or bladders, which are very large, exceeding when expanded the bladder proper, are present in neither land nor sea turtles. They are also wanting, according to Lesueur, in the *Trionychidae*. He found them in twelve American species of *Emydidæ*, and in two species of *Chelydridæ*, namely, in *Chelydra serpentina* and *Chelydra lacertina* Schweigg. (*Chelydra lacertina* Boulenger). Bibron and Dumeril (3) and Schweigger, as well as Strauch, found them in *Chelydra lacertina* Schweigg. Lesueur (10) called these bladders "lumbar vessels or auxiliaries." Duvernoy (7) believed that they are only in part comparable with the "glandulæ anales" of carnivorous mammals. He says: "This comparison is permissible on account of the shape and position, and perhaps in accordance with the plan of general composition of the whole organism, but is not admissible when a comparison of the details of their structure and their function is made; they are by no means organs with glandular walls forming a reservoir for secreted fluid." According to Duvernoy these bladders, to which he gives the name "accessory vessels," are very large, and the expansion of either of them equals that of the bladder alone. Their form is oval or cylindrical, and their position such that they must become compressed by the muscles of the lower belly, and may also be compressed by the posterior extremities, when the animal withdraws these into its carapace. M. Lesueur (10) found that

by blowing air into the living animal through the cloaca he could enlarge these vessels so much that they compelled the animal to project its extremities from its carapace and spread them out. The wall of the bladders is, according to Duvernoy (7), very thin, and is composed of two layers — an outer peritoneal layer, which is very rich in blood vessels, and an inner mucous membrane. He did not detect muscle fibers. He ascribes to these bladders a most peculiar function: “the animal can fill them with water, perhaps also with air, and can make use of them in diminishing its specific gravity. Hence we can explain why they are not found in land tortoises, which are not aquatic animals, and why they are absent even in the sea turtles, since the bodies of the animals are broad and flattened, and their extremities transformed into pinnate feet, and since, moreover, the specific gravity of sea water is greater than that of fresh water, they can dispense with the means of floating.”

It is even comprehensible, as Duvernoy (7) shows, that they should be absent in *Trionychidae*. In these turtles the extremities form strong rudders, as in the *Emydidae*, and their bodies are broad and flattened, thus enabling them to swim and float with ease. Lesueur (10) states that in *Cistudo carolina* (*Terrapene carolina* Linné, according to Strauch) these bladders are very small, and Duvernoy (7) concludes from this statement that their manner of living is the mean between that of the land turtles and the *Emydidae*. Stannius (16) merely says of these bladders, that, at least in the families *Testitudinidae* and *Emydidae*, a pair of sacs open into the cloaca. Owen (13), who calls them “cloacal sacculi,” considers them to be only transitory structures. Budge (5) critically examined them in *Cistudo amboinensis* Gray (*Terrapene amboinensis* Daudin, according to Strauch) (*Cyclemis amboinensis* Boulenger), and found them in both sexes. He calls them “anal bladders.” They consist of two membranes; the peritoneum appears to make up only the outer surface of the organ; and next to the posterior part of the bladder wall he finds an oblique striated muscle, which proceeds from the carapace and extends nearly up to the muscular cloaca. Here it becomes sinewy and forms a ligament, which

partly unites with that of the other side, partly diverges to the tendinous ligament which is seen in the middle line of the cloaca. The peritoneal covering continues over on to the anal bladders and unites, by means of a fold, with the part of the peritoneum which overspreads the posterior surface of the bladder. By means of the two membranous expansions before and behind, each bladder becomes surrounded as with a loop which must draw itself together as soon as the above-mentioned muscle contracts. According to Budge (5) it is very improbable that these "anal bladders" are true bladders and serve for the reception of urine. The true bladder has the shape and structure of the homologous organ in other vertebrates, but the "anal bladders," as Budge (5) shows, seem not to possess anything like a muscle sheath. As we have seen, Stannius (16), in opposition to Duvernoy, states that the "Bursae anales" are not only found in the *Emydidae*, but also in the land tortoises. In the *Emydidae* Hoffman (9) found them in the male as well as in the female of *Clemmys* and *Emys*. He examined these bladders and distinguished in them three layers — a peritoneal layer, a muscle-fiber layer, and a mucous membrane. The muscle-fiber layer is very strongly developed and permits great expansion and vigorous contraction. He says: "What the function of these bladders may be has remained entirely unknown to me." According to him they are wanting in the sea turtles, *Chelonia imbricata* Schweigg. (*Chelone imbricata* Boulenger) and *Chelonia viridis* Temm and Schleg (*Chelone mydas* Boulenger). In the *Chelydidae* he found them in *Chelemys victoria* Gray (*Emydura krefftii* Boulenger), *Chelodina longicollis*, and *Chelys fimbriata*. In the last-named species they are very large and very thin-walled.

Of the *Trionychidae* he examined a male of *Trionyx aegyptiacus* Geoffr. and a female of *Trionyx sinensis*. The "accessory bladders" were present in the male of *Trionyx aegyptiacus* Geoffr. (*Trionyx triunguis* Boulenger), and were distinguished by their unusually thin walls, as in *Chelys fimbriata*. They were not present in the female of *Trionyx sinensis* Wiegman. He says the occurrence of these "anal bladders" in the *Trionychidae* shows that the view of Duvernoy is incorrect.

In *Testudo graeca* the "anal bladders" are wanting, at least in the male. He does not say whether they are present or not in the female, as he had no opportunity to examine a female specimen.

Rathke (15) claims to have found the so-called "after bladders" (*Bursae anales*), which, like the bladder, empty into the cloaca, only in *Emys europaea* Schweigger (*Emys orbicularis* Boulenger) and *Emys lutaria* Schweigger (*Emys orbicularis* Boulenger). In the young animals they were, as regards size, like the bladder in the adult.

In my own investigations I endeavored to secure species of as many different families of *Testudinata* as possible, and these distributed over a wide area. I examined in all thirty animals, representing sixteen species, ten genera, and five families. The fresh material was obtained in the vicinity of Chicago and from Connecticut, Georgia, and Mississippi. I also had the use of preserved specimens which were collected in Australia by Dr. Semon, of Jena, Germany, and sent to the late Dr. Baur, Associate Professor of Paleontology in the University of Chicago.

I have followed Boulenger's classification and nomenclature except for the American box tortoises. In mentioning species of this genus I have used Dr. Baur's terminology.

This work was done in Hull Zoological Laboratory under the direction of Dr. W. M. Wheeler, to whom I acknowledge my great indebtedness for valuable criticisms and suggestions.

I found large "accessory bladders" in both sexes of the following North American species: *Chelydra serpentina*, *Chrysemis picta*, *C. rubriventris*, *Malacoclemmys terrapen*, *Clemmys insculpta*, *Clemmys guttata*, *Emys blandingii*.

The following Asiatic and Australian species possessed large "anal bladders": *Cyclemis dhor* ♀, *Cyclemis amboinensis* ♀, *Clemmys japonica* ♀, *Chelodina longicollis* ♀, *Emydura krefftii* ♀, *Emydura latisternum* ♀.

The North American species, *Terrapene carolina*, ♂ and ♀, and *Terrapene triunguis*, ♂ and ♀, have very small "accessory bladders." In the latter, which had never before been examined, I found very rudimentary "accessory bladders" much

smaller than those of *T. carolina*. In both species the size and appearance of these bladders indicate that they have become functionless.

In general it may be said that the "accessory bladders" are large oval or cylindrical sacs, opening dorsally on each side of the cloaca, near its anterior end. They lie in the pelvic region and extend into the peritoneal cavity, covered by the peritoneum. In some species the lungs are in contact with a large portion of their upper surfaces. By means of a fold which comes between their openings, a part of the cloaca in front of them can be closed off, so that the bladders may communicate directly with the cloaca, thus completely excluding all the other openings except the anus. In many of the fresh specimens these bladders were found to contain a clear liquid. When empty their external surface is corrugated like that of the true bladder, and their internal mucous membrane is thrown into folds.

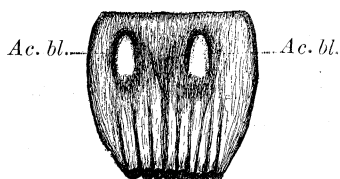


FIG. 1. — External dorsal view of the cloaca of *Terrapene carolina*, showing the size of the accessory bladders.

In regard to the minute structure of the "accessory bladders" the following data may be given: The "accessory bladders" have a muscular wall lined with a mucous membrane and covered with a serous coat. The muscular coat is made up of three layers, the inmost being incomplete. The principal fibers are longitudinal and circular, and the latter are arranged in bundles. Sections of the bladder and "accessory bladders" of *Chrysemis picta*, *Chelydra serpentina*, and *Emys blandingii* were made and compared. The mucous membrane is lined with epithelial cells which are arranged in layers. The cylindrical cells in the upper layer are very long and narrow. They gradually become more slender below, and again show expansions where the nuclei lie. The protoplasm of these cells is very finely granular. Three to four rows of round cells lie between the narrow projections of the cylindrical cells. The mucous membrane of the bladder is lined with epithelial cells which have a structure and arrangement similar to that of the

cells in the "accessory bladders." This similarity is best seen in camera lucida drawings of sections of the bladder and of the "accessory bladders."

### THE FUNCTION OF THE ACCESSORY BLADDERS.

As is well known, the habitat of the group of animals called *Testudinata* is diversified. Some species are exclusively terrestrial, others are more or less amphibious, and still others

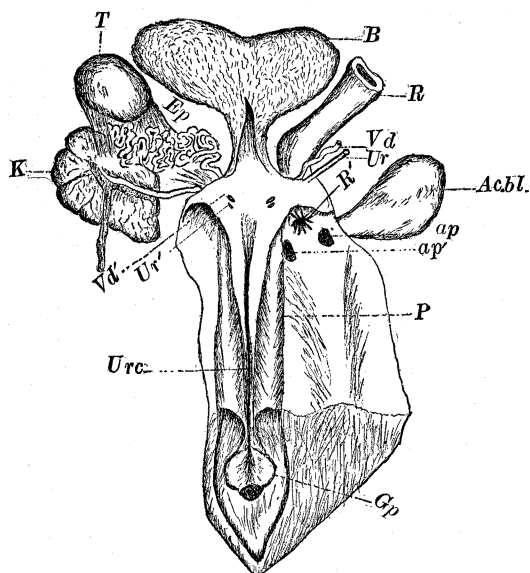


FIG. 2.—Male Urinogenital Organs of *Emys blandingii*. — *K.*, kidney; *Ur.*, ureter; *Ur.1*, aperture of ureter into the cloaca (*cl.*); *B.*, urinary bladder; *R.*, rectum; *R.1*, opening of rectum into the cloaca; *Ac. bl.*, accessory bladder; *ap.* and *ap.1*, apertures of the accessory bladders into the cloaca; *T.*, testis; *Ep.*, epididymis; *Vd.*, vas deferens; *Vd.1*, openings of the vasa deferentia into the cloaca; *Gp.*, glans penis; *Urc.*, urinogenital canal; *P.*, penis.

are aquatic. The presence or absence of "accessory bladders" in these animals appears to be, in a measure, correlated with their habits and environments. Lesueur (10) found that the "accessory bladders" were not present in land tortoises. I, too, have found these organs very small or entirely absent in the land species which I have examined (*Testudo polyphemus*, *Terrapene carolina*, and *Terrapene triunguis*).

C. Müller (12), who had frequent opportunities of observing

box tortoises in freedom as well as in captivity, found that they exhibited great aversion for water when placed in it, and always quitted it as quickly as possible. I have also observed that *Terrapene*, which is a decidedly terrestrial Emydid and has very rudimental "accessory bladders," is very uneasy when placed in water. It is generally believed that they never seek water but live wholly on vegetable matter, and obtain sufficient

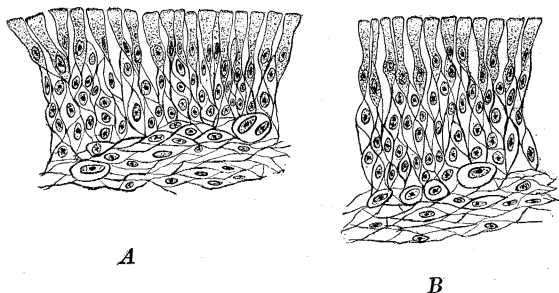


FIG. 3. — Sections through the bladder (A) and the accessory bladder (B) of *Emys blandingii*, showing the epithelial lining of these organs.

water from this source to maintain life. It would seem that the terrestrial mode of life of these tortoises may be an important factor in leading to a disappearance of the "accessory bladders."

Lesueur (10) again states that the "accessory bladders" are wanting in the *Cheloniidae* and *Trionychidae*.

Hoffman (9), too, says they are not present in the *Cheloniidae*, but are found in the *Chelydidae*. He claims they are present in one species of the *Trionychidae*, but this seems doubtful since no other investigator is found to support this statement. As before stated, I have examined several species of aquatic families, *Cinosternidae*, *Trionychidae*, and *Chelydidae*, and have found no "accessory bladders" in species of the first two families, but they were well developed in three species of the last.

The *Cinosternidae* and *Trionychidae* are purely aquatic and carnivorous in habit, and rarely go on land except to deposit their eggs in the sand on the shore near the water's edge.

I quote the following remarks concerning the *Chelydidae* from a letter received from Dr. Richard Semon: "*Chelodina*



*longicollis*, *Emydura krefftii*, and *Emydura latisternum* were all observed and caught by me in the Burnette River in Australia. They were taken in the middle course of the river. All three species live in those portions of the river where the water runs more slowly, and where the water plants are most abundant, in the so-called 'water holes' of the colonists. They are exclusively carnivorous, their diet consisting of all kinds of water animals. All three species are very rapacious. They often snatched the bait from the hooks which I had left dan-

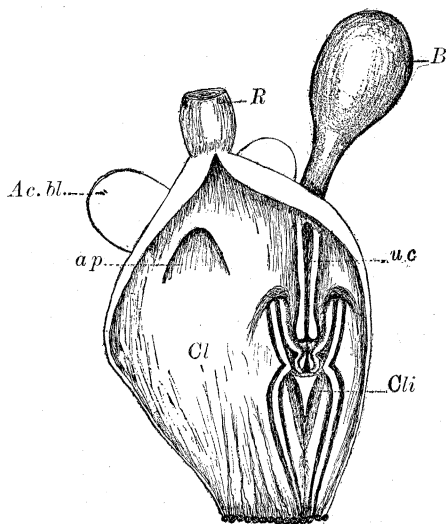


FIG. 4 shows in part the urinogenital organs of a young female *Chelodina longicollis*. — R., rectum; B., bladder; Ac. bl., accessory bladders with a common aperture, ap.; u. c., deep urinogenital canal; Cli., clitoris; Cl., cloaca.

gling in the water or on the bottom. I have rarely seen the animals on land. When disturbed *Chelodina longicollis* does not draw its head back straight in under the carapace, but folds it over to one side."

W. A. Haswell (8) found that the turtles of genus *Chelodina* have the habit of lying on the bottom of rivers and of drinking and then ejecting the water.

H. T. McCooen (11) states that the female of the genus *Chelodina* often goes a distance of three hundred meters on land to lay her eggs. She carries at least half a liter of water

and discharges it at intervals to soften the ground, that she may dig a hole about 18 cm. deep for her eggs. If this is not sufficient, she brings a second supply of water next morning and continues digging. The above account suggests that this genus may be amphibious in habit, and when more is known concerning the habits of the other genera of this family, they too may be found to be amphibious. The amphibious turtles, as their name implies, spend a part of their time on land, and often make considerable overland trips from stream to stream and from pond to pond in search of their food, which is both vegetable and animal, or in search of a suitable place to deposit their eggs.

Agassiz (1) says that "turtles (especially land and fresh-water turtles), like frogs, usually carry with themselves a quantity of water in the cloaca." According to the observations of Prof. J. Wyman (18) this water is taken up through the anus.

Anderson (1) says that some *Chelonia* draw in and eject water from the cloaca. In different species of the Southern Asiatic *Emydidae* he often found the cloaca dilated with water, which they ejected in jets when they drew in their limbs and tail, as they usually do when suddenly taken from the water. He made an examination, immediately after death, of about one hundred specimens of this family which has "accessory bladders," but in no case did he find the organs distended with water. My own observations were made immediately after the death of the animals, and, as I have before stated, I found a liquid in the "accessory bladders" of *Emys blandingii*, *Chelydra serpentina*, and *Chrysemis picta*.

Darwin (6), speaking of the *Testudo nigrata*<sup>1</sup> of the Galapagos Islands, says :

"It is pretty well ascertained that the bladders of frogs serve as a reservoir in which to carry the moisture necessary to their existence. This function may be ascribed to these turtles. When killed some days after their visit to the springs of the island, the bladders were found distended with stored up liquid. The inhabitants, if thirsty while in the low grounds,

<sup>1</sup> This species of tortoise has no "accessory bladders."

use this condition to their advantage. They kill a turtle and drink the contents of the bladder." He (Darwin) saw one dead in which the liquid was clear and had a slight brackish taste.

The following observations on the Galapagos turtles I take from Dr. Baur's article in the *American Naturalist* (1889):—

"Porter, in his general description of the Galapagos tortoises, says: 'They require no provisions or water for a year, nor is any further attention to them necessary than that their shells should be preserved unbroken (p. 214). They carry with them a constant supply of water in a bag at the base of the neck, which contains about two gallons; and on testing that found in those we killed on board, it proved perfectly fresh and sweet.' In regard to the bag of water, Porter gives another statement (p. 100). He partly ascended a hill on Charles Island, and on his way back he found a large tortoise. 'It was opened with the hope of finding some water to allay our thirst. But we were disappointed,' says he, 'in only finding a few gills of a disagreeable-tasted liquid.' The tortoises taken in James Island had in their stomach or reservoir from one to two gallons of a 'taste by no means disagreeable.' It seems, therefore, that this 'water reservoir' is not always filled. Captain Benjamin Morrell, who visited the islands in 1825, says: 'I have had these animals on board my own vessels from five to six months without their once taking food or water; and on killing them I have found more than a quart of sweet fresh water in the receptacle which nature has furnished them for this purpose!'"

Townson (17) experimented with *Emys europaea* by placing the animal in colored water and then in clear water, and saw the colored water returned through the cloaca. He says: "Without doubt this colored water was taken into the 'accessory bladders.'" I have made several experiments with *Chrysemis picta* similar to that recorded by Townson, but I did not find any indication that the colored water was taken in through the cloaca and then ejected from it. I also made post-mortem examinations of each animal and found no trace of colored water in the "accessory bladders." The fact that Townson used in his experiment turtles of a different genus from the one which I used may explain the difference in our results.

These circumstances suggest that these "anal bladders" are related to the habits of the animals which have them, for in considering their distribution, as shown by these observations, it is plain that they are restricted to turtles which are semi-terrestrial and semi-aquatic, and those forms which are exclusively terrestrial and those which are exclusively aquatic do not possess them. And it would appear that it is due to the presence of these bladders in amphibious turtles like *Chrysemis picta* and *Emys blandingii*, that they can live under more varied conditions than such terrestrial and aquatic forms as *Terrapene carolina* and *Cinosternum odoratum*, for apart from these "anal bladders," there is no very great difference between the general structure of an *Emys* and a *Terrapene*.

From my own observations I conclude that the "accessory bladders" of *Testudinata* function as reservoirs or receptacles for liquid stored up for the use of the animal.

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